

# Symmetry and order parameter dynamics of the human odometer

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**Abstract** Bipedal gaits have been classified on the basis of the group symmetry of the minimal network of identical differential equations (alias *cells*) required to model them. Primary bipedal gaits (e.g., walk, run) are characterized by dihedral symmetry, whereas secondary bipedal gaits (e.g., gallop-walk, gallop-run) are characterized by a lower, cyclic symmetry. This fact has been used in tests of human odometry (e.g., Turvey et al. in *P Roy Soc Lond B Biol* 276:4309–4314, 2009, *J Exp Psychol Hum Percept Perform* 38:1014–1025, 2012). Results suggest that when distance is measured and reported by gaits from the same symmetry class, primary and secondary gaits are comparable. Switching symmetry classes at report compresses (primary to secondary) or inflates (secondary to primary) measured distance, with the compression and inflation equal in magnitude. The present research (a) extends these findings from overground locomotion to treadmill locomotion and (b) assesses a dynamics of sequentially coupled measure and report phases, with relative velocity as an order parameter, or equilibrium state, and difference in symmetry class as an imperfection parameter, or detuning, of those dynamics. The results suggest that the symmetries and dynamics of distance measurement by the human odometer

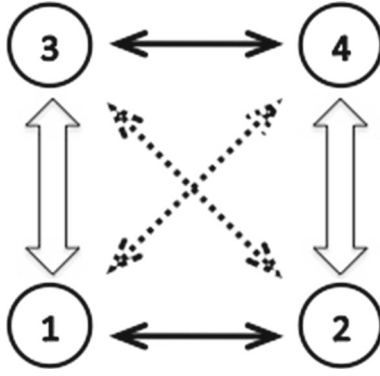
are the same whether the odometer is in motion relative to a stationary ground or stationary relative to a moving ground.

**Keywords** Bipedal symmetries · Odometry · Equilibria · Detuning

## 1 Introduction

For legged locomotion, idiothetic (nonvisual) information about movement is available with respect to the surface of support and with respect to inertial space (the general background of resistance to acceleration) (Mittelstaedt and Mittelstaedt 2001). In Gibson's (1966) classification of perceptual systems, the substrate variant of idiothetic information is detected by the haptic perceptual system and the inertial variant is detected by the basic orienting system (statocyst, vestibular organ). The substrate variant seems to be the more general basis for a non-visual ability to measure traveled distance (Etienne et al. 1998), an ability common to humans (Isenhower et al. 2012; Klatzky et al. 1990; Mittelstaedt and Mittelstaedt 2001; Schwartz 1999; Turvey et al. 2009), dogs (Séguinot et al. 1998), fiddler crabs (Walls and Layne 2009), spiders (Barth 2004; Seyfarth and Barth 1972), and desert ants (Wittlinger et al. 2006, 2007; Wohlgemuth et al. 2001).

A typical test for idiothetic distance perception, alias odometry, comprises two phases, measure ( $M$ ) and report ( $R$ ). Legged locomotion from a fixed starting point  $A$  to a variable terminus  $B$  is  $M$ . Legged locomotion from  $B$  in reproduction of the  $A - B$  distance is  $R$ . Participants during  $M$  and  $R$  are unsighted (humans might be blindfolded, ants might be in darkness). In Schwartz's (1999) seminal work, the  $A - B$  distance varied from 5 to 50 m. In  $M$ , human participants either walked (with the aid of a long cane) or ran (with the aid of a sighted partner). In  $R$ , participants walked



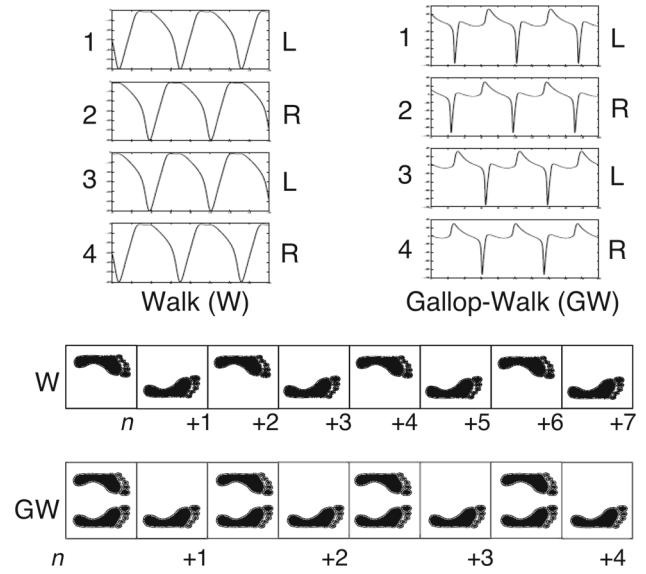
**Fig. 1** Network of four coupled identical cells (circles) with three types of coupling (arrows)

alone with the aid of a long cane. Schwartz found that  $R$  distance equaled  $M$  distance for both  $M$  by walking and  $M$  by running, and this was so despite the fact that the  $M$  variants differed in duration and number of steps as well as in gait details.

An important and challenging implication of research subsequent to Schwartz (1999) is that understanding human odometry requires a consideration of  $M$  gait in relation to  $R$  gait. For experimental distances of 7.6, 15.2, and 22.9 m, Turvey et al. (2009) confirmed Schwartz's (1999) finding that walk-walk and run-walk were equivalent  $M - R$  conditions (see also Izenhower et al. 2012), but showed that it was a special case. They did so by manipulating the symmetry classes of bipedal gaits identified by Pinto and Golubitsky (2006).

Formal analyses by Golubitsky and colleagues (Golubitsky et al. 1998, 1999; Golubitsky and Stewart 1999) reveal that to encompass the gaits exhibited by bipeds, quadrupeds, hexapods, etc., one requires a network of twice as many identical cells (central pattern generators, oscillators) as the animal has legs. The periodic solutions of these coupled cells, each expressed as a system of ordinary differential equations, come in two symmetry types: spatial (fixing the solution at each point in time) and spatio-temporal (fixing the solution only after a phase shift). For bipedal locomotion, let cells 1 and 3 regulate the left leg and cells 2 and 4 regulate the right leg (see Fig. 1). Then, the bipedal network's symmetry group consists of transpositions  $\rho$ ,  $\tau$ , and  $\rho\tau$  that swap (or transpose) pairs (12) and (34), pairs (13) and (24), and pairs (14) and (23), respectively (Pinto 2007; Pinto and Golubitsky 2006).

A primary bipedal gait (walk, run, slow two-footed hop, fast two-footed hop) is one for which the spatio-temporal symmetries satisfy the dihedral group  $D_2$  (see Pinto and Golubitsky 2006; Pinto 2007; Turvey et al. 2009, 2012). All three transpositions are entailed. A secondary bipedal gait (skip, gallop-run, gallop-walk, hesitation-walk) is one for which the spatio-temporal symmetries approximate the cyclic group  $Z_2$  (see Pinto and Golubitsky 2006; Pinto

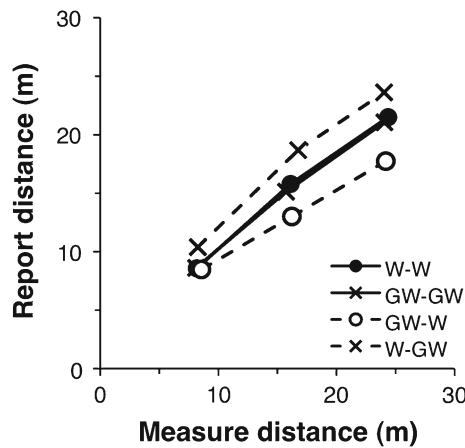


**Fig. 2** Upper panels. Periodic solutions for walk (W) and gallop-walk (GW) with 1–4 the cells in Fig. 1 and  $L$  and  $R$  referring to left and right limbs, respectively. (Numerical simulations adapted with permission from Pinto CMA, Golubitsky 2004 <http://www.math.uh.edu/~mg/reprints/papers/biped32.pdf>). Lower panel. Footfall patterns of W and GW. For W, 7 steps from the  $n$ th step are shown. For GW, 4 steps from the  $n$ th step are shown. Depicted distances covered are not intended to be equal. From Figure 3 of Turvey et al. (2012) with permission

2007; Turvey et al. 2012). Only one transposition is entailed. Figure 2 compares a  $D_2$  gait (walk) with a  $Z_2$  gait (gallop-walk). It shows the distinction between them in respect to their periodic solutions and their footfall patterns. The walk (W) and gallop-walk (GW) are the two gaits compared in the present research.

Returning to the human odometer findings of Turvey et al. (2009), if the  $M$  and  $R$  gaits are both primary, or if they are both secondary, then  $R$  distance =  $M$  distance, but if the  $R$  gait differs from the symmetry class of the  $M$  gait, then  $R$  distance  $\neq$   $M$  distance. (The conclusion was based on  $M - R$  gait pairings drawn from the primary gaits of walk, run, and backward-walk and the secondary gaits of gallop-walk, hesitation-walk, and gallop-run). In particular, as shown in Fig. 3, if the  $R$  gait is not in the same symmetry class as the  $M$  gait, then  $R$  distance is compressed (“undershoots”) when  $M$  gait is primary and  $R$  gait is secondary, and  $R$  distance is inflated (“overshoots”) when  $M$  gait is secondary and  $R$  gait is primary, with the degrees of  $R$ -distance compression and  $R$ -distance inflation equal in magnitude (Turvey et al. 2012).

The preceding can be summarized in these terms: In the human odometry task,  $M$  gait and  $R$  gait are so coupled as to comprise a system that is symmetric when  $M$  gait and  $R$  gait are of the same kind (both  $D_2$  or both  $Z_2$ ), and asymmetric otherwise. When the  $M - R$  system is symmetric, it might be said that  $R$  is in phase with  $M$  ( $R$  gait and  $M$  gait are equal). When the  $M - R$  system is asymmetric, it might be said that  $R$  is out of phase with  $M$  ( $R$  gait and  $M$  gait are unequal; of



**Fig. 3** Relation of  $R$  distance to  $M$  distance for the two symmetry-invariant  $M-R$  systems (W-W, GW-GW) and the two symmetry-variant  $M-R$  systems (GW-W, W-GW) as reported in [Turvey et al. \(2012\)](#)

positive sign when  $R$  gait is  $D_2$  and of negative sign when  $R$  gait is  $Z_2$ ). In what follows, we identify a dynamical system befitting the foregoing characterization of human odometry and we report an experiment by which it can be evaluated.

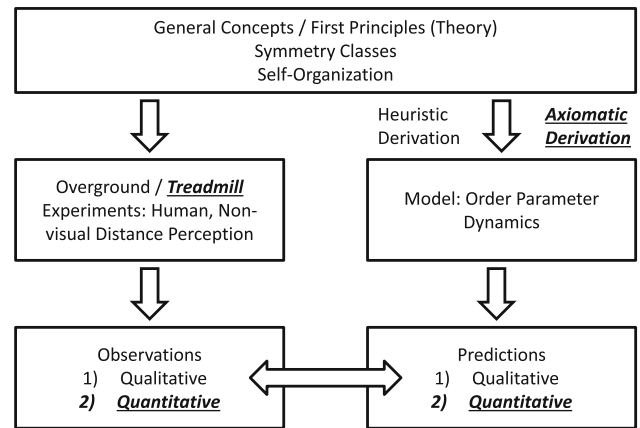
## 2 Overview

Figure 4 is a schematic of the preceding and present research (identified by italics) on the human odometer. Group symmetry analysis of bipedal gait ([Pinto and Golubitsky 2006](#)) and principles of self-organizing systems, as expressed in order parameter dynamics (e.g., [Frank 2005](#); [Haken 1977, 1983](#); [Kelso 1995](#)), provide the general concepts and theoretical underpinning for the experimentation and modeling. The preceding research investigated odometry overground (precisely, the floor of a gymnasium). In the present research, odometry is investigated on a treadmill. Further, whereas the preceding research derived the order parameter model of the  $M-R$  system via heuristic considerations, the derivation of the model in the present research is axiomatic. That is, it is derived from principles that are assumed to hold irrespective of the locomotion system, the mechanical details of its coordinative rhythmic states, and its perceptual control.<sup>1</sup> Such principles might be referred to as *first principles*.

The motivation for transferring the odometry task from an overground setting to a treadmill setting<sup>2</sup> was twofold, practical and theoretical. The practical aspect was ease of determining the order parameter directly from experimental

<sup>1</sup> A similar axiomatic approach has been taken previously to derive the relevant dynamical evolution equations known to govern bi-manual rhythmic coordination ([Frank et al. 2012b](#)).

<sup>2</sup> Another primary motivation was the difficulty of scheduling a university gymnasium facility during weekdays.



**Fig. 4** Schematic of method and theory in previous and present experiments on the human odometer

observations. In the treadmill setting, all model parameters can be estimated from experimentally observed movement trajectories. With estimates of the model parameters at hand, *quantitative* model predictions can be compared with experimental data. The theoretical aspect was the invariance of human odometry. Does human odometry in the treadmill setting with vision abide the same principles as human odometry in the overground setting without vision?<sup>3</sup> Or, synonymously, does sighted locomotion under conditions in which the ground moves relative to a person exhibit the same symmetries and dynamics of distance measurement as unsighted locomotion under conditions in which a person moves relative to the ground? The question was addressed by repeating Turvey et al.'s (2012)  $M-R$  manipulations in the treadmill setting. It would be answered positively by a replication of Fig. 3.

## 3 Axiomatic approach to $M-R$ system dynamics

To reiterate, odometry for humans and other animals is a matter of measuring a distance (e.g., from home to food source) and reproducing/reporting that measure. In the laboratory, the measure  $M$  and the report  $R$  can both be conducted without benefit of vision. When so conducted, experiments (e.g., [Isenhower et al. 2012](#); [Turvey et al. 2009, 2012](#)) suggest that  $M$  and  $R$  should be conceived as two components of a single system. Here we present an axiomatic basis for deriving the model of the  $M-R$  system developed heuristically in [Turvey et al. \(2012\)](#). It shares with the recent theoretical efforts of [Cruse and Wehner \(2011\)](#) the goal of addressing aspects of animal navigation as emergent properties of a decentralized

<sup>3</sup> Comparisons of treadmill and overground walking are mixed. Reports of differences in temporal gait parameters and leg kinematics (e.g., [Alton et al. 1998](#)) are countered by reports of sameness (e.g., [Lee and Hidler 2008](#); [Riley et al. 2008](#)).

system. It differs from those efforts by its focus on principles that are presumed to apply equally to both inanimate and animate dynamics.

### 3.1 Axiom 1: The coordination axiom

An  $M - R$  system, with asynchronous  $M$  and  $R$  activities, is a dynamical analogue of coordination between two synchronous activities. The notion of the  $M - R$  system as a sequential coordination problem suggests itself when measurement and report involve the same kind of fundamental physical modality such as body movement.

### 3.2 Axiom 2: The self-organization axiom

The second axiom is inspired by various approaches to the self-organization of so-called muscular synergies or coordinative structures—components undergoing orderly time variations in parallel (e.g., [Beek et al. 1995](#); [Haken 1996](#); [Kelso 1995](#); [Turvey 2007](#)). Axiom 2 is a claim that sequentially coordinated  $M$  and  $R$  activities emerge from a self-organization process subjected to the given task constraints.

### 3.3 Axiom 3: The order parameter axiom

Self-organizing systems such as lasers and convection cells exhibit amplitude variables that characterize their spatio-temporal dynamics. These amplitudes, referred to as order parameters, allow for a low-dimensional, macroscopic description of the high-dimensional microscopic behavior of such systems ([Haken 1977](#)). Given Axiom 2, we should expect  $M - R$  systems to be similarly characterized. Axiom 3 is the assertion that an order parameter exists for  $M - R$  systems.<sup>4</sup>

### 3.4 Axiom 4: The relative velocity (as order parameter) axiom

The fourth axiom claims that the relevant order parameter for the self-organized  $M - R$  system is the relative velocity in event time. Here, event time is a time scale appropriate for comparing events that differ in duration ([Turvey et al. 2012](#)). As such, event time is a mapping from laboratory time to another time scale that is attached to an individual experimental event. By convention, the event time scale starts at an event time of 0 with the beginning of the event and ends at an event time of 1 when the event is finished. The symbol  $t_e$  can be

<sup>4</sup> For physical systems (e.g., lasers, convection cells), order parameters have been identified by means of bottom-up approaches, that is, by means of mechanistic modeling ([Haken 1977](#)). In other instances, typically biological, order parameters have been suggested based on a top-down modeling approach, one based on experimental observations (e.g., [Frank et al. 2009, 2012a](#); [Haken 1996](#); [Kelso 1995](#)).

used to denote event time. Of particular significance, velocities observed in laboratory time can be mapped to velocities observed in event time. The latter velocities index how much distance is covered in a fraction of the event (e.g., at a given moment, a participant may move with a velocity of 1m per 1 % of the event duration). Relative velocity in event time is then defined as the difference between velocities of  $R$  and  $M$  given in event time. Let  $v$  denote relative velocity in event time. The variable  $v$  is a useful order parameter because it can be related directly to perceived distance estimation errors. In the case of a stationary velocity dynamics,  $v = 0$  implies that  $R$  distance is equal to  $M$  distance. In contrast,  $v < 0$  implies that  $R$  distance is compressed (“undershoots”) relative to  $M$  distance and  $v > 0$  implies that  $R$  is inflated (“overshoots”) relative to  $M$ .

### 3.5 Axiom 5: The symmetry axiom

The final axiom deals with two different types of symmetries: the group symmetries  $D_2$  and  $Z_2$  describing gait properties (see Sect. 1) and the left–right symmetry with respect to  $v = 0$  of the potential  $V$  of the order parameter dynamics. The symmetry axiom states that breaking the group symmetry in the  $M - R$  system (e.g., the  $M$  gait is  $W$ , the  $R$  gait is  $GW$ ) corresponds to breaking the left–right symmetry with respect to  $v = 0$  of the potential  $V$  such that the parameter  $\delta$  becomes different from zero.<sup>5</sup>

## 4 Experimental methods

### 4.1 Participants

Fourteen undergraduate students (8 females and 6 males; age range between 18 and 22 years old) at the University of Connecticut participated in the experiment in partial fulfillment of a course requirement. Participants provided informed consent. The university’s institutional review board approved the experimental protocols.

### 4.2 Materials

We used a Trackmaster TMX-425 treadmill (180kg capacity, running surface of  $76 \times 160$  cm, speed range 0.22 to 5.36 m/s). A goniometer was attached to each knee (Delsys<sup>TM</sup> Bag-noli Desktop System) and a wireless sensor, tracked by two fixed receptors (Liberty Latus<sup>TM</sup> wireless motion tracking system), was attached to the participant’s back. The receptors were mounted on a wooden frame located at one side of

<sup>5</sup> For a detailed discussion of the challenges posed for a principled derivation of imperfection parameters (detuning) see Appendix B in [Turvey et al. \(2012\)](#).

the treadmill. The goniometers measured knee angles (sampling frequency 1,000 Hz), and the wireless sensor captured the spatial position of the participant's back (sampling frequency 188 Hz) with respect to the coordinates defined by the arrangement of the receptors. The experiment was run at a treadmill speed of 1.35 m/s. At this speed, participants were (a) able to do W and GW at ease, and (b) not inclined to switch to a jog.

#### 4.3 Procedure

Treadmill locomotion by W or GW was performed with eyes open. Prior to the experiment, participants were instructed on performing GW. They were instructed to step forward with the dominant foot, then bring the other foot into alignment with the dominant foot and to repeat this after a pause (see Fig. 2). They were then given practice doing W and GW on the treadmill, and with mounting and dismounting from the treadmill, before proceeding with the actual trials. Each participant performed a total of 12 trials (three trials for each distance and four trials for each *M* gait-*R* gait condition, i.e., W-W, GW-GW, W-GW and GW-W). All participants were instructed to try to not use a way to quantify the distance (e.g., counting the number of steps) during *M*.

Each trial was conducted as follows. The participant was assigned W or GW as the *M* gait for a certain distance (the *M* distance) signaled by the experimenter (9, 18 or 27 m).<sup>6</sup> The participant then dismounted the treadmill and, after a brief pause (approximately 20–30 s), remounted the treadmill under the instruction to reproduce the *M* distance by either W or GW. To emphasize, the assignment of the *R* gait was given to the participant subsequent to *M*.

For each trial, the experimenter signaled the beginning and the end of *M*. However, the experimenter signaled only the beginning of *R* and the participant had to end the trial when he or she felt that *R* distance equaled *M* distance. No feedback on a participant's performance was given at any time during the experiment. Although participants were allowed to use the treadmill's handrails for any reason (e.g., feeling unsafe, discomfort with the treadmill's speed), none did. The entire experimental session lasted approximately 50 min.

#### 4.4 The order parameter equation

Order parameter equations are typically first order differential equations with the right-hand side interpreted as a force acting on the order parameter pushing it toward its stable fixed point (assuming that such a fixed point exists) (Haken

1977, 1983). In the context of such first order dynamical equations, force terms can be described as gradient forces of potential functions  $V$ . With respect to  $v$ , the order parameter equation assumes the form

$$\frac{d}{dt_e} v = -\nabla V(v) \quad (1)$$

where the nabla symbol stands for the derivative with respect to  $v$ . For *R* distance = *M* distance, the two forces that act on  $v$  (preventing overshoot and undershoot) are assumed to be in balance. This is consistent with a potential  $V(v)$  that exhibits left-right symmetry with respect to  $v = 0$ . In this case, the Taylor expansion of the potential function  $V(v)$  reads

$$V(v) = av^2 + bv^4 + \dots \quad (2)$$

The potential exhibits even terms only, where  $a$  and  $b$  are expansion coefficients. In contrast, in the case of *R* distance  $\neq$  *M* distance, the two aforementioned forces are unbalanced. This is consistent with a violation of the symmetry with respect to  $v = 0$ . In this case, the Taylor expansion of the potential reads

$$V(v) = a'v + av^2 + b'v^3 + bv^4 + \dots \quad (3)$$

and also contains odd terms. In particular, the parameter  $a'$  is assumed to be different from zero such that the fixed point of Eq. (1) is shifted from zero and the stationary  $v$  is either  $v > 0$  or  $v < 0$ . Taking a parsimonious approach (or alternatively assume that  $v$  is relatively small), only the lowest order terms, the terms with coefficients  $a'$  and  $a$ , may be considered. Introducing  $\delta = -a'$  and  $\gamma = a$ , Eq. (1) reads

$$\frac{d}{dt_e} v = \delta - \gamma \cdot v \quad (4)$$

A mathematical analysis of Eq. (4) reveals that the dynamics of  $v$  has a fixed point at  $v = \delta/\gamma$ . The fixed point is stable if  $\gamma > 0$  and unstable if  $\gamma < 0$ . In particular, the parameter  $\gamma$  is the negative value of the so-called Lyapunov exponent (Haken 1977; Strogatz 1994) of the fixed point. Therefore, for stable fixed points (featuring positive  $\gamma$ ) the parameter  $\gamma$  is a measure of attractor strength. The full order parameter model needs to account for fluctuations in the order parameter  $v$ . To this end, the model is supplemented with a fluctuating force (Schöner et al. 1986) given in terms of the product of a time-dependent normalized Langevin force (Frank 2005; Risken 1989) denoted by  $\Gamma$  and a weight parameter  $Q > 0$  (often referred to as noise amplitude.<sup>7</sup>) In doing so, Eq. (4) becomes

$$\frac{d}{dt_e} v = \delta - \gamma \cdot v + \sqrt{Q} \cdot \Gamma(t_e) \quad (5)$$

<sup>6</sup> These were the target distances. Actual distances differed slightly from these target distances (see Table 2) due to variation in the experimenter's signaling of when to stop and variation in the participant's ability to stop on cue.

<sup>7</sup> In the following Eq. (5),  $Q$ 's dimensions can be determined conveniently from the associated Fokker-Planck equation (Frank 2005; Risken 1989).



**Table 1** Variables in modeling the  $M - R$  system with dimension in event time units (ETU)

Variable	Description	Dimension
$t_e$	Event time	ETU
$v$	Relative velocity in event time	m/ETU
$\delta$	Imperfection parameter	m/ETU <sup>2</sup>
$\gamma$	Attractor strength	1/ETU
$Q$	Noise amplitude	m <sup>2</sup> /ETU

Equation (5) was used to conduct the model-based, quantitative analysis of the  $M - R$  system.<sup>8</sup> The variables of the model defined by the equation and their dimensions are summarized in Table 1.

#### 4.5 Post-analysis of sensor data

Goniometer data were evaluated to determine the number of steps performed by participants during  $M$  and  $R$  phases. During all experimental trials, the wireless sensor recorded the position data in the three dimensions of the participant on the treadmill. Only the times series  $x(t)$  of the participant's movements in the direction of locomotion was used in the analysis. The velocity of the participant in the laboratory frame was determined by taking the derivative of the recorded time series  $x(t)$ . The velocity was transformed into the coordinate systems of the participant. Subsequently, velocity trajectories as seen from the participant's perspective were transformed from laboratory time into event time, both for  $M$  and  $R$  phases. The difference between the  $R$  and  $M$  phase event time velocities yielded the relative velocity in event time, that is, the order parameter  $v$ . Order parameter trajectories were used to estimate the parameters  $\delta$ ,  $\gamma$  and  $Q$  of the model. (See "Appendix" for details). The difference between the  $R$  and  $M$  traveled distances from the participant's perspective yielded the perceived distance estimation error.

#### 4.6 Factorial designs of $M - R$ analysis

We hypothesized that the principles of human odometry observed previously would transfer from overground locomotion to treadmill locomotion. In order to investigate this hypothesis, distance estimation error was analyzed within

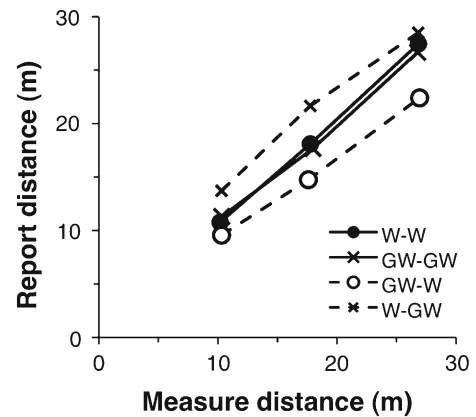
<sup>8</sup> Qualitatively, Eq. (5) reproduces the  $M - R$  distance results of Turvey et al. (2012) summarized in the final two paragraphs of the present Introduction. This can be seen by noting that the stationary mean relative velocity  $v_m$  is given by the fixed point:  $v_m = \delta/\gamma$  of Eq. (4), i.e., the deterministic part of Eq. (5). Consequently, for  $\delta = 0$ ,  $\delta > 0$ , and  $\delta < 0$ , the model exhibits mean relative velocities of  $v_m = 0$ ,  $v_m > 0$ , and  $v_m < 0$ , and predicts the distance relations of  $R = M$ ,  $R > M$ , and  $R < M$ , respectively.

the 3-factorial design used in Turvey et al. (2012). That is, the  $R$ -distance minus  $M$ -distance difference was subjected to a 3 (target distance)  $\times$  2 ( $R$  gait)  $\times$  2 ( $M - R$  gait symmetry) repeated-measures analysis of variance (ANOVA). In view of prior results, and in anticipation that distance did not qualitatively influence the effect of the symmetry difference between primary (e.g., W) and secondary (e.g., GW) gaits, the second (modeling) goal of the study was investigated within a  $2 \times 2$  factorial design in which data were collapsed across  $M$  distance. That is, the estimated model parameters  $\delta$ ,  $\gamma$  and  $Q$  were subjected to three separate 2 ( $R$  gait)  $\times$  2 ( $M - R$  gait symmetry) repeated-measures ANOVA. For sake of completeness such an ANOVA was also conducted for the distance estimation error (the difference between  $R$  distance and  $M$  distance). Two planned comparisons for the two  $R$  gaits were conducted on  $\delta$  to test the hypothesis that  $\delta$  was larger when the  $M$  and  $R$  gaits belonged to different symmetry classes. For sake of completeness the same planned comparisons were also conducted on the difference between  $R$  distance and  $M$  distance.

## 5 Results

Figure 5 shows  $M$  and  $R$  distances for all experimental conditions. Table 2 summarizes the distance measures and Table 3 summarizes the corresponding number of steps, a quantity used in the determination of the low-pass filter frequency (see "Appendix").

As shown in Fig. 5 and Table 2, for the symmetry invariant  $M - R$  systems, the  $R$  distances (mean 18.67 m) closely matched the  $M$  distances (mean 18.31 m). In contrast, as shown in Figure 5 and Table 2, for the symmetry variant  $M - R$  systems,  $R$  distance (mean 15.57 m) was less than  $M$  distance (mean 18.28 m) for GW-W, and  $R$  distance (mean



**Fig. 5** Relation of  $R$  distance to  $M$  distance for the two symmetry invariant  $M - R$  systems (W-W, GW-GW) and the two symmetry variant  $M - R$  systems (GW-W, W-GW) in the present experiment

**Table 2**  $M$  and  $R$  distance means and standard deviations (m) as a function of target distance (m) for the symmetry invariant and symmetry variant  $M - R$  systems

Target (m)	$M - R$ system							
	Symmetry invariant				Symmetry variant			
	W-W		GW-GW		GW-W		W-GW	
	$M$	$R$	$M$	$R$	$M$	$R$	$M$	$R$
9	10.19 $\pm$ 0.78	10.77 $\pm$ 2.18	10.32 $\pm$ 1.01	11.32 $\pm$ 2.38	10.31 $\pm$ 1.76	9.57 $\pm$ 4.55	10.31 $\pm$ 0.64	13.72 $\pm$ 5.50
18	17.76 $\pm$ 0.54	18.10 $\pm$ 3.03	17.98 $\pm$ 0.71	17.67 $\pm$ 2.47	17.60 $\pm$ 0.37	14.75 $\pm$ 4.70	17.75 $\pm$ 0.36	21.65 $\pm$ 5.66
27	26.84 $\pm$ 0.60	27.46 $\pm$ 3.26	26.78 $\pm$ 0.86	26.67 $\pm$ 2.86	26.94 $\pm$ 0.75	22.40 $\pm$ 5.79	26.83 $\pm$ 0.52	28.51 $\pm$ 6.40

**Table 3** Mean number of  $M$  and  $R$  steps for the symmetry invariant and symmetry variant  $M - R$  systems

Target (m)	$M - R$ system							
	Symmetry invariant				Symmetry variant			
	W-W		GW-GW		GW-W		W-GW	
	$M$	$R$	$M$	$R$	$M$	$R$	$M$	$R$
9	8.9	10.2	9.2	10.4	10.3	8.4	9.1	13.4
18	16.7	14.6	16.1	16.9	14.7	13.8	14.2	20.1
27	24.7	22.8	22.2	26	23.7	20.5	21.1	24.5

21.29 m) was greater than  $M$  distance (mean 18.29 m) for W-GW.

The 2 ( $M - R$  Symmetry)  $\times$  2 ( $R$  Gait)  $\times$  3 ( $M$  Distance) repeated-measures ANOVA conducted on the  $R$  distance minus  $M$  distance magnitude revealed a significant main effect of  $R$  Gait  $F(1, 12) = 10.48, p < 0.01$  with GW as  $R$  Gait associated with  $R$  distance  $> M$  distance ( $M = 1.59, SD = 0.62$ ) and with W as  $R$  Gait associated with  $R$  distance  $< M$  distance ( $M = -1.1, SD = 0.75$ ). No significant main effects of  $M - R$  Symmetry and  $M$  distance were found. Of the possible interactions, only  $M - R$  Symmetry  $\times R$  Gait was significant,  $F(1, 12) = 5.47, p < 0.05$ .

Figure 6 shows distance error ( $R$  distance minus  $M$  distance),  $\delta$ ,  $\gamma$ , and  $Q$  of the model for the two  $R$  gaits (W and GW) as a function of whether  $M$  and  $R$  gaits are the same (symmetric  $M - R$  system) or different asymmetric  $M - R$  system). Figure 6a gives the distance estimation error as a function of  $R$  gait (RG in the figure) and  $M$  gait- $R$  gait symmetry. The distance estimation errors for symmetric  $M-R$  systems, W-W and GW-GW, were less than 1m on average ( $M = 0.51$  m,  $SD = 2.59$  and  $M = 0.19$  m,  $SD = 2.43$ , respectively). In contrast, distance estimation errors for the asymmetric  $M - R$  systems, W-GW and GW-W, were approximately 3m on average ( $M = 2.99, SD = 5.80$  and  $M = -2.71, SD = 4.92$ , respectively). The two-way ANOVA showed a main effect for  $R$  Gait,  $F(1, 41) = 12.47, p < 0.001$ , and a significant  $R$  Gait  $\times M - R$  Sym-

metry interaction,  $F(1, 41) = 25.97, p < 0.0001$ . The distance estimation error was larger for GW-W than for W-W,  $t(41) = 3.86, p < 0.001$ , and larger for W-GW than for GW-GW,  $t(41) = 3.231, p < 0.005$ .

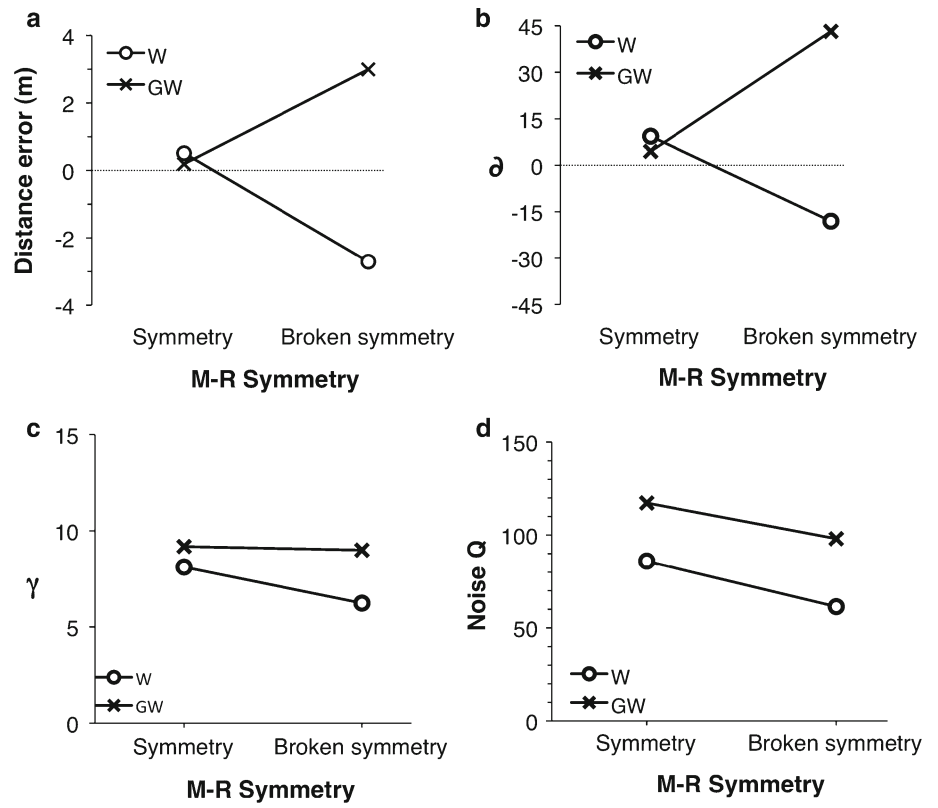
Figure 6b depicts  $\delta$  as a function of  $R$  Gait and  $M - R$  Gait Symmetry. The pattern of results for  $\delta$  was similar to the pattern observed for the distance estimation error. The two-way ANOVA for  $\delta$  showed a significant main effect of  $R$  Gait,  $F(1, 41) = 7.28, p < 0.01$ , with GW associated with overall positive  $\delta$  ( $M = 23.81, SD = 12.57$ ) and W associated with overall negative  $\delta$  ( $M = -4.34, SD = 6.38$ ). Likewise significant was  $R$  Gait  $\times M - R$  Gait Symmetry,  $F(1, 41) = 16.08, p < 0.0001$ . Planned comparisons showed that the differences in  $\delta$  between  $M - R$  symmetric and  $M - R$  asymmetric were significant:  $t(41) = 2.65, p < 0.01$  for W as  $R$  gait and  $t(41) = -0.29, p < 0.005$  for GW as  $R$  gait.

The estimated model parameters  $\gamma$  (attractor strength) and  $Q$  (noise) are depicted in Fig. 6c, d. Figure 6c suggests that all four values of  $\gamma$  were positive, that all four attractors were stable, suggestions confirmed by a planned comparison with a test value of zero,  $t(167) = 11.12, p < 0.0001$ . The absence of main and interaction effects in the two-way ANOVA on  $\gamma$  suggests, further, that the four attractors were stable to the same degree. Finally, although Fig. 6d is consistent graphically with  $Q$  larger for GW as  $R$  gait than W as  $R$  gait, the two-way ANOVA revealed the difference to be nonsignificant.

## 6 Discussion

The primary goal of the present research was to address the question of whether human odometry—specifically, measuring a distance by legged locomotion and reproducing that distance by legged locomotion—is an instance of self-organization, an instance of synergy formation. The hypothesized formative process is three tiered. It is at the scale of a *complete step* from toe push off to heel strike (a synergy of neural and biomechanical components that differ in tim-

**Fig. 6** Mean values of Eq. (5) parameters as a function of  $R$  Gait and symmetry of  $M - R$  system



ing and spacing). It is at the scale of a *complete two-steps sequence* (a synergy constituting same left and right steps as in W or different left and right steps as in GW). It is at the scale of a *complete journey  $M$*  distance plus  $R$  distance (a synergy of *two* two-steps sequences organized in series, with the two-steps sequences either of the same symmetry—that is, both  $\mathbf{D}_2$  or  $\mathbf{Z}_2$ —or of different symmetry—one two-steps sequence  $\mathbf{D}_2$ , the other  $\mathbf{Z}_2$ ). The answer to the self-organization question was sought in the form of an order parameter whose dynamics define the coordination of  $M$  gait and  $R$  gait.

### 6.1 Generality of bipedal gait symmetry classes

The search was made in the context of odometry of legged locomotion on a treadmill as opposed to overground. As highlighted, this context facilitated the acquisition of the necessary data. The experimental results underscore the generality of the group symmetry perspective on bipedal locomotion (Pinto 2007; Pinto and Golubitsky 2006). The formal distinction between W (primary gait) and GW (secondary gait) holds for both overground locomotion (without vision) and treadmill locomotion (with vision).

*Serial coordination (or coupling) versus parallel coordination (or coupling).* The order parameter dynamics in relative velocity Eq. (5) distinguished the symmetric  $M - R$  systems of the present experiment from the asymmetric  $M - R$

systems in terms of attractor location ( $v$ ) and detuning ( $\delta$ ) but not in terms of attractor strength ( $\gamma$ ) and associated noise ( $Q$ ). In parallel coordination (e.g., rhythmic coordination of two hand-held pendulums), the relative phase ( $\phi$ ) dynamics predicted by the Haken-Kelso-Bunz equation, and commonly verified, is that of coordinate changes in the four parameters: Deviation of  $\phi$  from  $0^\circ$  or  $180^\circ$  due to nonzero  $\delta$  is accompanied by  $\gamma$  decrease and  $Q$  increase (for summaries see Kelso 1995; Amazeen et al. 1998; Park and Turvey 2008).<sup>9</sup> There are a few notable exceptions.<sup>10</sup> Pellecchia et al. (2005) predicted that concurrent cognitive activity should decrease  $\gamma$ . To the contrary, they found that concurrent cognitive activity displaced  $\phi$  from  $0^\circ$  without reducing the MAXLINE quantity of Recurrence Quantification Analysis, an index of  $\gamma$ . Relatedly, Silva and Turvey (2012) inquired whether the relative orientation of the vectors representative of the mass moment distribution of body segments ( $v_{mm}$ ) of right and left hands ( $\Delta v_{mm} = v_{mm\text{ left}} - v_{mm\text{ right}}$ ) constitutes haptic information supporting bimanual coordination and, if so, how it contributes to coordination dynamics. They found that the sign and magnitude of  $\Delta v_{mm}$ , in particular of the first moment vector, systematically affected  $\phi$  but not  $\gamma$ .

<sup>9</sup> Such might well be the case for overground locomotion.

<sup>10</sup> For a theoretical overview see Frank et al. (2012a).



## 6.2 Odometry without legs

That the results of the present experiment, conducted with non-translational treadmill locomotion and eyes open, replicated those of the preceding experiments, conducted with translational ground locomotion and blindfolds, suggests that the proposed order parameter dynamics may be very general. Here we ask whether it might apply to the overground legless odometry reported by Berthoz and colleagues (Berthoz et al. 1995). For  $M$ , the blindfolded participant was seated in a four-wheeled robotic vehicle and transported passively in a forward direction to a distance of 2–10 m. For  $R$ , the blindfolded participant drove the vehicle in the same forward direction for a distance (perceived to be) equal to  $M$ . The regression of  $R$  distance on  $M$  distance was  $.86M + .47m$ . Applying this regression function to the  $M$  values of 9, 16 and 27 m of the present experiment yields  $R$  values of 8.21, 14.23, and 23.69 m, respectively. Comparing these pairs of  $M$  values and  $R$  values with those in the present Table 2 suggests a parallel between the legless odometry studied by Berthoz et al. and the GW-W condition of the present experiment. The parallel, in turn, allows the conjecture that the systematic undershooting was due to the robot—a system of lower order (lower symmetry)—providing  $M$ , and the participant plus robot—a system of higher order (higher symmetry)—providing  $R$ .<sup>11</sup>

The central theoretical feature of Berthoz et al. followed from the manipulation of the velocity profile of the  $M$  phase. In one experiment, it was triangular (peak velocity .6–1.0 m/s); in another experiment, it was trapezoidal or square. In both experiments, the participants reproduced the essential form of the  $M$  velocity profiles in the  $R$  phase despite the instructions to simply reproduce distance. A dynamical reading of this outcome is that  $M$  distance is stored as a velocity profile, a dynamic pattern of motion (*contra* a value in a cartesian-like cognitive map) that is reproduced as  $R$  distance (Berthoz et al. 1995; Berthoz and Viaud-Delmon 1999).

Equation (5) similarly suggests a dynamical reading of the present data, but with different emphases. Rather than viewing  $M$  distance as a memory and  $R$  distance as that which is guided by the memory, Eq. (5) suggests that  $M$  and  $R$  distances are episodes of a single event rendered so by the intention “measure then report” with a resultant coupling of  $M$  activity and  $R$  activity as a single dynamical system. As spelled out above in respect to Eq. (5), for  $\delta = 0$ ,  $\delta > 0$ , and

$\delta < 0$ , the dynamical model of legged odometry exhibits mean relative velocities of  $v_m = 0$ ,  $v_m > 0$ , and  $v_m < 0$ , and predicts the distance relations of  $R = M$ ,  $R > M$ , and  $R < M$ , respectively. The outcome  $R$  distance =  $M$  distance when  $\delta = 0$  can be said to express *time-translation invariance* (see Frank et al. 2009, 2012a). Nonzero values of the parameter  $\delta$  break the symmetry of Eq. (5) and induce time-translation variance—commonly referred to as “forgetting.” The preceding logic, derivative of notions of Encoding Specificity and Transfer Appropriate Processing in memory theory (Neath and Surprenant 2003), has been applied to the dynamically similar latent aftereffect in prism adaptation (see Dotov et al. 2013; Frank et al. 2009, 2012a).

## 6.3 Berkeley’s Hypothesis in the context of treadmill locomotion

Subsequent to Schwartz (1999), articles on human legged odometry have been framed in terms of an assertion by Berkeley (1709/1948, Section, 45, p. 188) in his *Essay Toward a New Theory of Vision*: Distance for the human is measurable by “the motion of his body, which is perceivable by touch.” The hypothesis suggested by the assertion is that legged locomotion from a location  $A$  to another location  $B$  is, in and of itself, specific to the distance from  $A$  to  $B$ . A very special kind of perceptual constancy of distance is presumed, one that holds over the speed with which, and the gaits with which (consider walking and running), a person traverses the ground between  $A$  and  $B$  without the aid of vision.

In the present experiment, an  $A$ -to- $B$  ground distance was absent as such and vision was present as such, albeit of minimal benefit to the measurement task. Treadmill locomotion provides a different test of Berkeley’s hypothesis. Patently, it is a case of the ground moving relative to the person rather than the person moving relative to the ground. The participant is being asked to determine how many meters of ground moved relative to him or her rather than how many meters he or she moved relative to the ground. The present research in conjunction with the prior research indicates that, with respect to gait symmetry, Berkeley’s hypothesis applies with equal force to both conditions of relative motion.

## Appendix

Details of parameter estimation method and self-consistency test for estimated parameter  $\gamma$

Let  $x_M(t)$  and  $x_R(t)$  denote the participant positions from the perspective of the participant during  $M$  and  $R$  phases, that is, distances traveled up to time  $t$ .  $x_M(t)$  and  $x_R(t)$  are defined on the intervals  $[0, T_M]$  and  $[0, T_R]$ , respectively, where  $T_M$  and  $T_R$  denote the durations of the  $M$  and  $R$  phases. This

<sup>11</sup> The Berthoz et al. experiment could be conducted with an  $M$  robot and an  $R$  robot, where  $M$  robot =  $R$  robot, or  $M$  robot <  $R$  robot, or  $M$  robot >  $R$  robot. The inequalities could be introduced by manipulating an extensive quantity, such as robot weight or robot width. According to Eq. (5), the two inequalities should have opposite effects. If one robot inequality yielded  $M$  distance >  $R$  distance, the other robot inequality should yield  $M$  distance <  $R$  distance, with robot equality yielding  $M$  distance =  $R$  distance.

“Appendix” shows how the model parameters were estimated from these trajectories.

The position trajectories  $x_k(t)$  for  $k = M, R$  involved two components, an oscillatory component (related to the pendulum like rhythmic activity) and a directed, forward motion component. In a first approximation, it was assumed that both components added up linearly to the observed motion. The order parameter model in the text addressed the directed motion component. To remove the oscillatory component the trajectories  $x_k(t)$  were subjected to a low-pass filter with filter frequency determined by the number of steps (see e.g., Table 3). Explicitly, the filter frequency was determined as the step frequency (derived from the number of steps and  $T_k$ ) minus an offset of 2 Hz. Subsequently, the low-pass filtered trajectories were numerically differentiated with respect to  $t$  to obtain the velocities  $v_k(t)$ .

Let  $y_k(t_e)$  denote the position trajectories in event time with  $k = M, R$ . Then, from  $t_e = t/T_k$  for  $k = M, R$  it follows that  $y_k(t_e) = x_k(t_e \cdot T_k)$ . Let  $u_k(t_e)$  denote the velocity in event time defined as the derivative of  $y_k$  with respect to  $t_e$ . Then, using the chain rule of differentiation, we see that  $u_k(t_e) = T_k \cdot v_k(t_e \cdot T_k)$ . Consequently, the velocities of M and R phases in event time were calculated using  $u_k(t_e) = T_k \cdot v_k(t_e \cdot T_k)$  and the velocity trajectories  $v_k(t)$  mentioned above. Subsequently, the relative velocity in event time was calculated as the difference  $u(t_e) = u_R(t_e) - u_M(t_e)$ . In order to avoid an inflation of symbols, we replaced in the main text  $u(t_e)$  by  $v(t_e)$ .

From the Ornstein–Ühlenbeck model defined by Eq. (5), it follows that in the stationary case the expectation value (ensemble average) of  $v(t_e)$  equals the ratio  $\delta/\gamma$ . Therefore, the ratio  $\delta/\gamma$  was estimated from the time-average  $v_m$  of  $v(t_e)$  assuming that ensemble averaging can be approximated by time-averaging (ergodicity assumption). In addition,  $v_m$  was subtracted from the trajectory  $v(t_e)$  and in doing so a centered trajectory with zero mean value was generated. The time-discrete version of the Ornstein–Ühlenbeck with zero mean value corresponds to an autoregressive (AR) model of order 1. Therefore, the model parameters of the Ornstein–Ühlenbeck model,  $\gamma$  and  $Q$ , were estimated using the Yule-Walker method (Diggle 1990) for the AR – 1 model. Let  $a_1$  denote the first autoregressive parameter and VAR denote the variance of the noise term of the AR – 1 model. Then, a detailed calculation shows that  $\gamma$  and  $Q$  can be determined from  $a_1$  and VAR as follows:

$$\begin{aligned}\gamma(estim) &= \frac{1 - a_1(estim)}{\Delta t_e} \\ Q(estim) &= \frac{VAR}{2\Delta t_e}\end{aligned}\quad (6)$$

Here  $\Delta t_e$  denotes the single time step of the event time grid obtained from the laboratory time  $t$ . To reiterate, the Yule-Walker method yielded the AR – 1 parameters  $a_1$  and

VAR. Subsequently,  $\gamma$  and  $Q$  were calculated from Eq. (6). Having obtained  $\gamma$ , the parameter  $\delta$  was calculated from the estimated ratio  $\delta/\gamma$ , that is, from  $v_m$ , according to

$$\delta(estim) = v_m \cdot \gamma(estim) \quad (7)$$

As a self-consistency test, the parameter  $\gamma$  was estimated in an alternative way, namely, from the power spectrum of  $v(t_e)$ . In a first step, the power spectrum of a given trajectory  $v(t_e)$  was calculated. Subsequently, the analytical solution of the power spectrum (Diggle 1990) of an Ornstein–Ühlenbeck process was fitted to the observed spectrum using a nonlinear best-fit method (MATLAB function `nonlfit`). In doing so, a second estimate for  $\gamma$  was obtained.

In summary, for each pair of  $M$  and  $R$  phases two estimates for the parameter  $\gamma$  were obtained: one estimate from Eq. (6) involving the Yule-Walker method and another one via power spectral analysis. The two scores for  $\gamma$  were compared by a  $t$  test for dependent samples. The  $t$  test was not statistically significant indicating that the parameter estimation method involving the Yule-Walker method for the AR – 1 model produced consistent results with the power spectral analysis method tailored to an Ornstein–Ühlenbeck process.

## References

- Alton F, Baldey L, Caplan S, Morrissey MC (1998) A kinematic comparison of overground and treadmill walking. *Clin Biomech* 13: 434–440
- Amazeen P, Amazeen EL, Turvey MT (1998) Dynamics of human intersegmental coordination: theory and research. In: Collyer C, Rosenbaum D (eds) *Timing of behavior: neural, psychological and computational perspectives*. MIT Press, Cambridge, pp 237–260
- Barth FG (2004) Spider mechanoreceptors. *Curr Opin Neurobiol* 14:415–422
- Beek PJ, Peper CE, Stegeman DF (1995) Dynamical models of movement coordination. *Hum Mov Sci* 14:573–608
- Berthoz A, Israël I, Georges-François P, Grasso R, Tsuzuku T (1995) Spatial memory of body linear displacement: What is being stored? *Science* 269:95–98
- Berthoz A, Viaud-Delmon I (1999) Multisensory integration in spatial orientation. *Curr Opin Biol* 9:708–712
- Cruse H, Wehner R (2011) No need for a cognitive map: decentralized memory for insect navigation. *PLoS Comput Biol* 7:e1002009. doi:10.1371/journal.pcbi.1002009
- Diggle PJ (1990) *Time series: a biostatistical introduction*. Clarendon Press, Oxford
- Dotov DG, Frank TD, Turvey MT (2013) Balance affects prism adaptation: evidence from the latent after effect. *Exp Brain Res* 231:425–432
- Etienne A, Berlie J, Georgakopoulos J, Maurer R (1998) Role of dead reckoning in navigation. In: Healy S (ed) *Spatial representation in animals*. Oxford University Press, Oxford, pp 54–68
- Frank TD (2005) *Nonlinear Fokker-Planck equations: fundamentals and applications*. Springer, Berlin
- Frank TD, Blau J, Turvey MT (2009) Nonlinear attractor dynamics in the fundamental and extended prism adaptation paradigm. *Phys Lett A* 373:1022–1030
- Frank TD, Blau J, Turvey MT (2012a) Symmetry breaking analysis of prism adaptation’s latent aftereffect. *Cogn Sci* 36:674–697

- Frank TD, Silva PL, Turvey MT (2012b) Symmetry axiom of Haken-Kelso-Bunz coordination dynamics revisited in the context of cognitive activity. *J Math Psychol* 56:149–165
- Gibson JJ (1966) The senses considered as perceptual systems. Houghton Mifflin, Boston
- Golubitsky M, Stewart I (1999) Symmetry and pattern formation in coupled cell networks. *Pattern Form Contin Coupled Syst* 115:65–82
- Golubitsky M, Stewart I, Buono P, Collins JJ (1998) A modular network for legged locomotion. *Physica D* 115:56–72
- Golubitsky M, Stewart I, Buono P, Collins JJ (1999) Symmetry in locomotor central pattern generators and animal gaits. *Nature* 401:693–695
- Haken H (1977) *Synergetics. An introduction*. Springer, Berlin
- Haken H (1983) *Advanced synergetics*. Springer, Berlin
- Haken H (1996) *Principles of brain functioning*. Springer, Berlin
- Isenhower RW, Kant V, Frank TD, Pinto CMA, Carello C, Turvey MT (2012) Equivalence of human odometry by walk and run is indifferent to self-selected speed. *J Mot Behav* 44:47–52
- Kelso JAS (1995) *Dynamic patterns*. Bradford/MIT Press, Cambridge
- Klatzky RL, Loomis JM, Golledge RG, Cicinelli JG, Doherty S, Pellegrino JW (1990) Acquisition of route and survey knowledge in the absence of vision. *J Mot Behav* 22:19–43
- Lee SJ, Hidler J (2008) Biomechanics of overground vs. treadmill walking in healthy individuals. *J Appl Physiol* 104:747–755
- Mittelstaedt ML, Mittelstaedt H (2001) Idiothetic navigation in humans: estimation of path length. *Exp Brain Res* 139:318–332
- Neath I, Surprenant A (2003) *Human memory*. Thompson/Wadsworth, Belmont
- Park H, Turvey MT (2008) Imperfect symmetry and the elementary coordination law. In: Fuchs A, Jirsa VK (eds) *Coordination: neural, behavioral and social dynamics*. Springer, Berlin, pp 3–25
- Pellecchia GL, Shockley K, Turvey MT (2005) Concurrent cognitive task modulates coordination dynamics. *Cogn Sci* 29:531–557
- Pinto CMA, Golubitsky M (2006) Central pattern generators for bipedal locomotion. *J Math Biol* 53:474–489
- Pinto CMA (2007) Numerical simulations in two CPG models for bipedal locomotion. *J Vib Control* 13:1487–1503
- Riley PO, Dicharry J, Franz J, Croce UD, Wilder RP, Kerrigan DC (2008) A kinematics and kinetic comparison of overground and treadmill running. *Med Sci Sport Exer* 40:1093
- Risken H (1989) The Fokker-Planck equation. *Methods of solution and applications*. Springer, Berlin
- Schöner G, Haken H, Kelso JAS (1986) A stochastic theory of phase transitions in human hand movement. *Biol Cybern* 53:247–257
- Schwartz M (1999) Haptic perception of the distance walked when blindfolded. *J Exp Psychol Hum Percept Perform* 25:852–865
- Séguinot V, Cattet J, Benhamou S (1998) Path integration in dogs. *Anim Behav* 55:787–797
- Seyfarth EA, Barth FG (1972) Compound slit sense organs on the spider leg: mechanoreceptors involved in kinesthetic orientation. *J Comp Physiol* 78:176–191
- Silva PL, Turvey MT (2012) The role of haptic information in shaping coordination dynamics: inertial frame of reference hypothesis. *Hum Mov Sci* 31:1014–1036
- Strogatz SH (1994) *Nonlinear dynamics and chaos*. Addison-Wesley, Reading
- Turvey MT (2007) Action and perception at the level of synergies. *Hum Mov Sci* 26:657–697
- Turvey MT, Romaniuk-Gross C, Isenhower RW, Arzamarski R, Harrison S, Carello C (2009) Human odometer is gait-symmetry specific. *P Roy Soc Lond B Bio* 276:4309–4314
- Turvey MT, Harrison SJ, Frank TD, Carello C (2012) Human odometry verifies the symmetry perspective on bipedal gaits. *J Exp Psychol Hum Percept Perform* 38:1014–1025
- Walls ML, Layne JE (2009) Direct evidence for distance measurement via flexible stride integration in the fiddler crab. *Curr Biol* 19:25–29
- Wittlinger M, Wehner R, Wolf H (2006) The ant odometer: stepping on stilts and stumps. *Science* 312:1965–1967
- Wittlinger M, Wehner R, Wolf H (2007) The desert ant odometer: a stride integrator that accounts for stride length and walking speed. *J Exp Biol* 210:198–207
- Wohlgemuth S, Ronacher B, Wehner R (2001) Ant odometry in the third dimension. *Nature* 411:795–798